

Naturæ' may doubtless be traced to this correspondence. The often voluminous descriptions, sometimes accompanied by drawings, which form enclosures or parts of the letters in question, have not been reproduced in the 'Naturhistorisk Tidsskrift,' as not having sufficient value in proportion to the space they would occupy. But as an instance of how the correspondence illustrates the systematic works of Linnæus, we may mention the following. In the second edition of 'Fauna Suecica' we find under the genus *Hydra* a species called *triticea*; but in the twelfth edition of the 'Systema Naturæ' this is omitted, and rightly so. From one of the letters of Fabricius we gather in what way Linnæus was led to correct the error; for Fabricius here communicates to him that a certain Schun (whose name is probably misspelt), minister at Bamf, had informed him that these supposed Hydras, which occur frequently on the coast, were only the ova of *Buccinum lapillus*, L. This letter is written from Edinburgh, 17 September, 1767 (Naturhistorisk Tidsskrift, vii. p. 459).

But as I have already said, it is for the appreciation of Linnæus's contemporaries and his influence on them (in short, of the Linnæan period in natural history) that this correspondence is principally valuable; and I may perhaps, in conclusion, be permitted to express a hope that some writer thoroughly qualified for the task may be found inclined to work up in an exhaustive manner the vast store of material for the history of science which I feel sure must be contained in this remarkable collection of letters.

Copenhagen, April 1874.



On the Classification of the Animal Kingdom. By T. H. HUXLEY,
LL.D., Sec. R.S., F.L.S., &c.

[Read December 3rd, 1874.]

IN the twelfth edition of the 'Systema Naturæ' Linnæus gives the following definition of the object of classification:—

"Methodus, anima scientiæ, indigitat primo intuitu, quodcunque corpus naturale, ut hoc corpus dicat proprium suum nomen, et hoc nomen quæcumque de nominato corpore beneficio seculi innotuere, ut sic in summa confusione rerum apparenti, summus conspiciatur Naturæ ordo" (*l. c.* p. 13).

While entertaining the same general conception of classificatory method, Cuvier saw the importance of an exhaustive analysis of the adult structure of animals. The most complete investigation of the kind ever made under the direction of a single mind, and far surpassing all previous attempts in extent and thoroughness, is contained in the 'Leçons d'Anatomie Comparée' and the 'Règne Animal.' Cuvier's classification is purely morphological; it is an attempt to enunciate the facts of structure determined in his time, and largely by his own efforts, in a series of propositions of which the most general are the definitions of the largest groups, and are connected by a series of subordinate, differential propositions with those which constitute the definition of the species.

In his great work, the 'Entwickelungs-Geschichte der Thiere,' Von Baer, among other contributions to science of first-rate importance, showed that our knowledge of an animal's true structure must be imperfect, unless we are acquainted with those developmental stages (which are successive structural conditions) through which the animal has passed in its way from the ovum to the adult state; and, since 1828, no philosophical naturalist has neglected embryological data in forming a classification.

In 1859, Darwin, in the 'Origin of Species,' laid a new and firm foundation for the theory of the evolution of living beings, which had been hypothetically sketched out by Lamarck, and thereby introduced a new element into Taxonomy. If a species, like an individual, is the product of a process of development, the character of that process must be taken into account when we attempt to determine its likeness or unlikeness to other species; and Phylogeny, or the history of the evolution of the species, becomes no less important an element than Embryogeny in the determination of the systematic place of an animal. The logical value of phylogeny, therefore, is unquestionable; but the misfortune is, that we have so little real knowledge of the phylogeny even of small groups, while of that of the larger groups of animals we are absolutely ignorant. To my mind there is full and satisfactory proof of the derivation of *Equus* from *Hipparion*, and of this from an Anchitherioid ancestor; and there is much to be said in favour of the derivation of other genera of existing Mammals from their Tertiary predecessors. There are also pretty clear indications of the series of changes by which the Ornithic arose out of the Reptilian type, and the Amphibian from the Fish; but I do not know that as much can be said of other large

groups. We are reduced to speculation—to the formation of more or less probable hypotheses; and, though I believe that phylogenetic speculations are of great interest and importance, and are to be reckoned among the most valuable suggestors of, and guides to, investigation, I think it is well to recollect, not only that they are at present, for the most part, incapable of being submitted to any objective test, but that they are likely long to remain in that condition. For the ultimate test of the truth of a phylogenetic hypothesis is the historic record of the succession of living forms contained in the fossiliferous rocks; and the present state of geology gives no encouragement to the supposition that even the whole series of fossiliferous rocks represents a period coextensive with the existence of life on the earth. In speculating on these subjects, it is constantly needful to remind oneself, even now, that there is every reason to believe that all the leading modifications of animal form were existent at least as early as the close of the Palæozoic epoch; and though it is true that the fossiliferous Palæozoic rocks are thicker than all the rest put together, yet the amount of progress in evolution from a moner to the fully differentiated Vertebrata of the Trias bears an enormously larger ratio to the amount of progress from the Triassic vertebrates to those of the present day. All such comparative measurements as these are but rough aids to the imagination; but the Invertebrata yield even stronger evidence in the same direction. The larger divisions of the Arthropoda were completely differentiated in the Carboniferous epoch; so were those of the Mollusks and those of the Echinoderms. The great desideratum is the discovery of estuarine and freshwater formations of Silurian, Cambrian, and Laurentian date. At the present moment, I do not think that any one is in a position to form even a probable guess as to what will be found in such deposits.

Taxonomy should be a precise and logical arrangement of verifiable facts; and there is no little danger of throwing science into confusion if the taxonomist allows himself to be influenced by merely speculative considerations. The present essay is an attempt to set a good example, and, without reference to phylogeny, to draw up a classification of the animal kingdom, which, as a fair statement of what, at present, appear to be well-established facts, may have some chance of permanence, in principle, if not in detail, while the successive phylogenetic schemes come and go. No doubt the increase of our knowledge of embryology will largely

modify any conclusions which may be based upon our present imperfect acquaintance with the facts of development; and, in many cases, it is impossible to do more than suggest the conclusions towards which these incomplete data tend.

Among those animals which are lowest in the scale of organization there is a large assemblage, which either present no differentiation of the protoplasm of the body into structural elements; or, if they possess one or more nuclei, or even exhibit distinct cells, these cells do not become metamorphosed into tissues—are not histogenetic. In all other animals, the first stage of development is the differentiation of the vitellus into division-masses, or *blastomeres*, which become converted into cells, and are eventually metamorphosed into the elements of the tissues. For the former the name PROTOZOA may be retained; the latter are coextensive with the METAZOA of Haeckel.

I. THE PROTOZOA.

The movements of the body are effected either by pseudopodia or by cilia, which latter may either be small and numerous, or long and single, and at most two. When pseudopodia are the only instruments of progression, the animal may be termed a *myxopod*; when numerous cilia, a *trichopod*; when single or double flagelliform cilia, a *mastigopod*.

Among the Protozoa, two groups are distinguishable:—1. The *Monera*; 2. The *Endoplastica*.

1. *The Monera*.—There is no “nucleus.” Our knowledge of these forms and of their relations is largely due to Haeckel, who has shown that several of them present a remarkable alternation of conditions. Thus, *Protamœba* is a myxopod which may become encysted, and, in that condition, divides into several portions which are set free and resemble the parent, or are myxopods. *Protozonas* is a *mastigopod* which becomes encysted, divides, and gives rise to myxopods, which subsequently become converted into *mastigopods*. *Myxastrum* is a myxopod which becomes encysted, divides, and the products of division become enclosed in ovoid cases, whence they emerge as myxopods. *Vampyrella* is a myxopod which devours *Gomphonema* and other stalked Diatoms, encysts itself on their stalks, divides, and gives rise to new myxopods. In *Protomyxa*, the primitively independent myxopods unite into plasmodia. Although our knowledge of the structure of the soft parts of the *Foraminifera* is imperfect, and the case of *Gromia* sug-

gests caution in assuming that they are all devoid of nuclei, it is probable that the great majority of the Foraminifera resemble *Protogenes* and belong to this division, the extent of which will doubtless be greatly enlarged by the discovery of new forms.

2. *The Endoplastica*.—The application of the term “nucleus” to the structure commonly so called in this division of the Protozoa, to a certain extent implies a belief in its being homologous with the histological element to which the same name is applied; and I prefer to revive a term I once proposed for the latter, and to call the body at present in question “endoplast.” It may or may not be the homologue of the histological nucleus; and without expressing any definite opinion on that subject, I wish to leave it open for further consideration.

It is remarkable that among these Endoplastica there is a series of forms which run parallel with the Monera. Thus *Amœba* is like a *Protamœba* with a nucleus and, commonly, a contractile vesicle. The Infusoria Flagellata are comparable to *Protomonas* with the same additions, and attaining a considerable degree of complexity in *Noctiluca*.

The Gregarinidæ repeat the series of forms of *Myxastrum*, though some become divided into several segments, and, as E. Van Beneden has shown, acquire muscular fibres.

The Acinetidæ and the Radiolaria apparently have their moneral representative in *Actinophrys sol*, though the conversion of the pseudopodia into suckers in the Acinetidæ distinguishes them remarkably.

On the other hand, while no moneral trichopod seems yet to have been discovered, the trichopod type is richly represented, in this division, by the Catallacta of Haeckel, and by the Infusoria Ciliata, of which I think the Catallacta should form only a subdivision.

It is among the Ciliata that the Endoplastica attain their greatest degree of complexity, by a process of direct differentiation of their protoplasmic substance into tissues and organs, without the intervention of cell-formation.

I have recently examined several genera of Infusoria (*Paramecium*, *Balantidium*, *Nyctotherus*, *Spirostomum*) with great care—using very high microscopic powers (1200–2000 diameters), employing osmic acid (which at once kills and preserves unchanged the tissues of the Infusoria) and other reagents, and comparing them with such truly cellular organisms of similar size

as *Opalina*; and I must express my entire agreement with Von Siebold and with Haeckel in their conclusion, that the protoplasm of these animals is not differentiated into cells.

At most there is an excessively minute, and sometimes regular, granular structure, which is found in the endoplast, as well as elsewhere, and appears to me to be altogether similar to that of the protoplasm between the nuclei of *Opalina*. But although the bodies of the Infusoria contain no cells, they may be differentiated into very definite tissues. In the genera mentioned, the so-called "cuticula" is, I believe, simply the transparent outermost layer of the protoplasm, and the cilia are directly continuous with it. Beneath this is a well-marked cortical layer, in which the "trichocysts" of *Paramecium* are situated, and which, in *Spirostomum*, *Balantidium*, and *Nyctotherus*, presents the distinct muscular fibres described by Stein and others. The inner substance is, in some (*Balantidium*, e. g.), semifluid, and undergoes an obvious rotation; but in *Nyctotherus*, not only is there no movement of this substance, but the long curved œsophagus is succeeded by an ill-defined region, which lies between it and the anus, is permanently filled with ingested matter, and is, in one sense, an alimentary tract. Even in *Paramecium*, the complex water-vessels, which lie, for the most part, not in the cortical layer, but beneath it, show, by the permanence of their disposition, that a great part of the inner substance is fixed. The constancy of position of the endoplast*, which also lies beneath, and not in, the cortical layer, is evidence to the same effect.

In comparing the Ciliated Infusoria with nucleated cells, the existence of the so-called "nucleolus," which assuredly can have nothing to do with the histological element so named, and which I propose to term the *endoplastula*, is an important fact, often left out of sight.

I have no observation to offer upon the vexed question of the nature of the endoplastula, as none of the numerous individuals of the different species named, which I have examined, showed the changes described by so many observers. That the endoplast itself is a reproductive organ is clear; but the development of embryos by its fission is an argument rather against, than in favour of, identifying it with the nucleus of a cell. No cell is known to multiply by fission of its nucleus alone.

* The membranous investment of the endoplast, so often described and figured, certainly has no existence in the unaltered state of the Infusoria I have mentioned.

On the whole, while I hesitate to absolutely identify the endoplast of an Infusorian with the nucleus of a histological cell, and can find no analogue for the endoplastula in the latter, I think that Von Siebold's view holds good, and that the higher Infusoria are unicellular animals, in the sense that *Mucor*, *Vaucheria*, and *Caulerpa* are unicellular plants.

Nevertheless it must be admitted, on the other hand, that though the view for which Ehrenberg has so long contended, that the *Infusoria* possess, in miniature, an organization, in a broad sense, as complex as that of the higher animals, is not tenable, the great majority of them are far more highly organized than was suspected before that indefatigable observer commenced his long and remarkable series of investigations.

II. THE METAZOA.

The germ undergoes differentiation into histogenetic cells; and these cells become arranged into two sets, the one constituting the outer wall of the body, while the other lies internal to the foregoing, and forms the lining of the alimentary cavity, when, as is usually the case, a distinct alimentary cavity exists. In the embryo, the representatives of these two layers are the *epiblast* and *hypoblast*. In the adult, they are the *ectoderm* and the *endoderm*, which answer to the *epidermis*, and the *epithelium* of the alimentary canal, in the higher animals.

All the Metazoa, in fact, commence their existence in the form of an ovum, which is essentially a nucleated cell, supplemented by more or less nutritive material, or *food-yolk*. The ovum, after impregnation, divides into blastomeres, giving rise to a *Morula* (Hæckel), in the midst of which arises a cavity, the *blastocœle* (*cleavage-cavity*, "*Furchungshöhle*" of the Germans), which may be larger or smaller, filled only with fluid, or occupied by food-yolk. When it is largest, the blastomeres, united into a single layer, form a spheroidal vesicle, enclosing a correspondingly shaped blastocœle. When it is reduced to a minimum, the *Morula* is an almost solid aggregation of blastomeres, which may be nearly equal in size, or some much larger than others, in consequence of having undergone less rapid division. The next stage in the development of the embryo of a Metazoon consists (in all cases except a few parasitic anenterous forms) in the conversion of the *Morula* into a body having a digestive cavity, or a *Gastrula*.

The conversion of the *Morula* into the *Gastrula* may take place in several ways.

In the simplest, the *Morula*, being composed of equal or nearly equal blastomeres, these, undergoing conversion into cells, differentiate themselves into an epiblast, which invests the remaining cells, constituting the hypoblast. The central cells of the hypoblast next diverge and leave a space filled with fluid, the alimentary cavity, which opens at one end, and thus gives rise to the *Gastrula*. This is the process generally observed in Porifera, Cœlenterata, Turbellaria, Trematoda, and Nematoidea.

In a second class of cases, the *Morula* becomes converted into blastomeres of unequal sizes, a small and a large set. The smaller are rapidly metamorphosed into cells, and invest the larger (with any remains of the food-yolk) as a blastoderm. The hypoblast arises either from the blastoderm thus formed, or from the subjacent larger blastomeres. This is the process observed in certain Turbellaria, in the Ctenophora, in most of the Oligochæta and Hirudinea, in the Arthropoda, and in most Vertebrata.

In a third group of instances, the *Morula*, whether consisting of equal or unequal blastomeres, becomes spheroidal, and encloses a correspondingly shaped blastocœle. One part of the wall of this vesicular *Morula* then becomes invaginated, and is converted into the hypoblast, which encloses the alimentary cavity, the latter communicating with the exterior by the aperture of invagination. This process has been observed in the Chatognatha, Echinodermata, and some Gephyrea, in *Lumbricus* and *Hirudo*—in polychætous Annelida, Enteropneusta, Brachiopoda, and most Mollusca—and in *Amphioxus*, *Petromyzon*, and the Amphibia among the Vertebrata.

The various modes in which the two primary layers of the germ may be developed shade off into one another, and do not affect the essence of the process, which is the segregation of one set of cells to form the external covering of the body, and of another to constitute the lining of the alimentary canal. We may, with Haeckel, term those animals which pass through the *Gastrula* stage, *Gastreæ*. The *Gastrula* may be deeply cup-shaped, or flattened out into a disk, slightly concave on one side; but in whatever manner the *Gastrula* is formed, and whatever be its shape when its alimentary cavity is complete, one of two things happens to it. It becomes provided with many ingestive apertures distinct from that first formed (polystomatous), or with one only,

which may or may not be distinct from the first aperture of the *Gastrula* (monostomatous).

Metazoa polystomata.—The former division comprises only the Sponges (Porifera or Spongida), in which, as the remarkable researches of Haeckel (" Monographie der Kalk-Schwämme ") have shown, the walls of the deeply cup-shaped *Gastrula* become perforated by the numerous inhalant ostioles, while the primitive opening serves as the exhalant aperture.

The latter division includes all the remaining forms, which may be grouped together as *Metazoa monostomata*. Among these, two primary groups are distinguishable, of which the second exhibits an advance in organization upon the first. In the first, the primitive aperture of the *Gastrula* becomes the permanent mouth (Archæostomata). In the second, the permanent mouth is a secondary perforation of the body-wall (Deuterostomata).

1. *The Archæostomata*.—It is now well established that the aperture of the *Gastrula* becomes the oral aperture of the adult in the Cœlenterata, which group includes animals differing much in grade of organization, from the simple *Hydra* to the complex *Ctenophore*, but all manifestly exhibiting variations of one fundamental type.

In most of the Hydrozoa, the ovum passes into a solid *Morula*, which, as in the Porifera, becomes differentiated into an epiblast and a hypoblast. The central cavity of the latter opens at one end, and thus far the *Gastrula* of the Hydrozoa is very like that of the sponges; but the aperture produced in this manner becomes the mouth; and if, as not unfrequently happens, apertures are formed elsewhere, they do not serve the purpose of taking in food. In such Hydrozoa as have thickened body-walls, hollow prolongations of the hypoblast extend into the blastocœle, and are surrounded by a mesoblastic tissue. These prolongations may become branched and anastomose, resembling vascular canals; but they remain permanently in connexion with the alimentary cavity. The reproductive elements are developed in the body-wall, and usually in cœcal outwardly projecting processes of that wall, which dehisce and set free the ova and spermatozoa upon the outer surface of the body.

The Actinozoa, while presenting the same continuity of the cavity of the body with the alimentary cavity which is exhibited by the Hydrozoa, differ from them in two respects. The commencement of the alimentary canal is, as it were, sunk in the

body; and the reproductive elements are developed in the walls of the gastrovascular canals, and pass into them on their way outwards.

The development of the coralligenous Actinozoa has not yet been thoroughly worked out; but Lacaze-Duthiers has shown that, in *Corallium rubrum* and other Gorgonidæ, the *Morula* passes into an elongated, almost vermiform, ciliated *Gastrula*, which becomes fixed by one end, and then develops the intermesenteric chambers. It can hardly be doubted that these are formed as diverticula from the basal end of the primitive alimentary canal, in which case the developmental process differs but little, essentially, from that of such a Hydrozoon as *Carmarina hastata*; and the line of demarcation between the Actinozoa and the Hydrozoa becomes very narrow.

The Ctenophora, on the other hand, differ somewhat in development, as in other respects, from the Coralligena. Their development has been carefully worked out by Kowalewsky and more recently by Agassiz.

The laid egg is contained in a spacious capsule, and consists of an external thin layer of protoplasm, which, in some cases, is contractile, investing an inner vesicular substance. The vitellus thus constituted divides into two, four, and, finally, eight masses; on one face of each of these the protoplasm-layer accumulates, and is divided off as a blastomere of much smaller size than that from which it arises. By repeated division, each of these gives rise to smaller blastomeres, which become nucleated when they have reached the number of 32, and form a layer of cells, which gradually spreads round the large blastomeres, and invests them in a complete blastodermic sac. At the pole of this sac, on the face opposite to that on which these blastoderm-cells begin to make their appearance, an ingrowth or involution of the blastoderm takes place, which, extending through the middle of the large yelk-masses towards the opposite pole, gives rise to the alimentary canal. This, at first, ends by a rounded blind termination; but from it, at a later period, prolongations are given off, which become the gastrovascular canals.

At the opposite pole, in the centre of the region corresponding with that in which the blastoderm-cells first make their appearance, the nervous ganglion is developed by metamorphosis of some of these cells.

It is clear that the invaginated portion of the blastoderm, which

gives rise to the alimentary canal, answers to the hypoblast, while the rest corresponds with the epiblast.

The large blastomeres which become enclosed between the epiblast and hypoblast in the manner described, appear to serve the purpose of a food-yolk; and the space which they originally occupied is eventually filled by a gelatinous connective tissue, which possibly derives its origin from wandering cells of the epiblast.

The Actinozoa and the Hydrozoa constitute the Cœlenterata, which are definitely characterized by the fact that, in all the higher forms, the mesoblast is traversed by canals formed by diverticula of the hypoblast, which permanently remain in continuity with the alimentary cavity, and that, in the lower forms, the alimentary cavity is prolonged into the cœnosarc. They are usually said to have a radiate symmetry; but, even in the *Actiniæ*, there are traces of bilaterality; and in the Ctenophora the bilateral symmetry of the adult is obvious.

Parallel with these may be ranged an assemblage composed of the Turbellaria, Rotifera, and Trematoda, the Nematodea, Oligochæta, and Hirudinea, to which the name of 'Scolecimorpha' may be applied. They are associated together by the closest resemblances of structure, and present an even greater range in grade of organization than the Cœlenterata. The lower Rhabdocœla come very close to the Infusoria (as close as the multicellular to the unicellular Algæ), and are but little superior to *Hydra* in the degree of their organic differentiation, while in the land-Planariæ, the Trematoda, and the Nemertidæ we have animals which attain a considerable complexity and, in the case of many Trematoda and of *Lineus (Pilidium)*, undergo remarkable metamorphoses. Such forms as *Dinophilus* appear to connect the rhabdocœle Turbellaria with the Rotifera. The lower Nematodea are extremely simple, while the higher are considerably differentiated; and, as Schneider has shown, they are connected with the Turbellaria by such forms as *Polygordius*. The Oligochæta and the Hirudinea either belong to this division, or constitute a transitional group between it and the Deuterostomata. In *Lumbricus* (and apparently in *Hirudo*) there seems to be no doubt that the aperture of invagination of the *Gastrula* becomes the mouth. According to Kowalewsky, the mouth in *Euaxes* and *Tubifex* is of secondary origin; but its close resemblance to that of the earthworm and of the leech embryos leads me to suspect that there must be some error of interpretation here. On the other hand, it may be that these

are transitional forms, such as we may expect to find bridging over the intervals between all groups, as knowledge widens. In any case, they differ from the foregoing in the development of a segmented mesoblast. In the Cœlenterata, Nematodea, Turbellaria, Trematoda, and Rotifera, the mode of origin of the cells which lie between the epiblast and the hypoblast, constitute the mesoblast, and give rise to the connective tissues and muscles of the body-wall and of that of the intestine, is not precisely known. They may take their origin in the epiblast or in the hypoblast, or in both. But, in the Earthworm and Leech, after the epiblast and hypoblast are differentiated, the cells of the latter give rise, by division, to two bands of cells which lie one on each side of the long axis of the ventral face of the worm, and constitute the mesoblast. This becomes marked out by transverse constrictions into segments, and, in each segment, gives rise to all the tissues which lie between the epiblast and hypoblast. The mouth corresponds with the primitive involution of the *Morula*; the anal aperture is a new formation.

In the Nematodea and in the lower rhabdocœle Turbellaria, the intestinal canal is a simple tube or sac. But, in some Turbellaria and Trematoda the alimentary canal gives off diverticula, which ramify through the mesoblast and even unite together, giving rise to a gastrovascular canal-system like that of the Cœlenterata. These animals, therefore, have what may be termed an *enterocœle*, more or less distinct from the proper digestive cavity, but connected with it, ramifying through the mesoblast.

Whether the remarkable group of worms termed Gephyrea by De Quatrefages (and including *Sipunculus*, *Sternaspis*, *Bonellia*, &c.) belong to the Archæostomata, or not, is uncertain, too little being known of the early stages of their development. They appear to me to be closely allied to the Rotifera (compare *Bonellia*, for example), to the Enteropneusta, and to the Echinodermata; while Schneider, by his very ingenious comparison of the *Phoronis*-larva *Actinotrocha* with *Cyphonautes*, affords even stronger grounds than those furnished by the structure of *Phoronis* itself, for suspecting that the Gephyrea and the Polyzoa are more intimately connected than has been supposed to be the case.

It will be observed that the Scolecimorpha present a series of modifications from the unsegmented Turbellaria and Nematodea, through the imperfectly segmented Rotifera, to the polymerous Oligochæta and Hirudinea, and that the segmentation primarily occurs in the mesoblast.

2. The *Deuterostomata*.—In the remaining *Gastrea* the embryo develops a secondary mouth as a perforation of the body-wall, the primary aperture sometimes becoming the anus and sometimes disappearing.

The *Schizocæla*.—Of these Metazoa *Deuterostomata* there are some which follow the mode of development of the *Oligochæta* and *Hirudinea* very closely, so far as the formation and segmentation of the mesoblast is concerned; though the question whether this segmented mesoblast arises from the epiblast or the hypoblast, has not been exhaustively worked out. These are the *Annelida Polychæta*.

It is a very general, if not universal, rule among these animals, that the *Gastrula* is formed by invagination, and that the aperture of invagination persists as the anus of the adult. Almost universally, again, the outer surface of the *Gastrula* is provided with cilia, by the working of which it is actively propelled through the water in which it lives; and these cilia usually become restricted to certain areas of the body, in the form of zones transverse to its long diameter. In this respect the larvæ of some *Gephyrea* present similar features. Moreover setæ, developed in involutions of the ectoderm, are very generally present, especially on the limbs, when such exist. Some are apodal; some possess symmetrically disposed setæ in each segment of the body; and in many, true though rudimentary limbs (*parapodia*), one pair for each segment of the body, occur. In a few of the highest forms (e. g. *Polynoë*) some of the anterior limbs are turned forwards, and lie at the sides of the mouth, foreshadowing the jaws of the *Arthropoda*. In some, a process of the ectoderm, in the region of the head, gives rise to a cephalic hood or mantle. A perivisceral cavity occupies the space between the wall of the body and that of the alimentary canal, and, so far as is known, is invariably formed in the substance of the mesoblast, by a sort of splitting or divarication of its constituent cells, whence it would seem to be a rehabilitation of the primitive blastocœle. The great majority of the *Polychæta* possess the so-called "segmental organs"—variously formed tubes, which open on the surface of the body, on the one hand, and, usually, into the perivisceral cavity on the other. Not unfrequently these, or some of them, play the part of conduits of the generative products.

The lower *Arthropoda* closely resemble the *Polychæta* in their development, except that the food-yolk is usually large, the ali-

mentary cavity is rarely formed by invagination, and cilia are never met with in any part of the body*. The mesoblast is developed and becomes segmented precisely in the same way. Limbs are formed and rarely remain rudimentary; usually they become jointed; and, in almost all cases, more or fewer of those which lie in the neighbourhood of the mouth are converted into jaws. The perivisceral cavity is formed in the same way as in the foregoing group; so that the Arthropoda, like the Polychæta, are "schizocœlous." In the higher Insecta, the embryogenetic process is complicated by the development of an amnion, which singularly resembles that met with in the higher Vertebrata. Mr. Moseley's recently published careful examination of *Peripatus* tends to show that this animal, formerly regarded as an Annelid, is really a low and primitive form of Arthropod, and thus affords evidence of the highest significance as to the relations of the Annelida with the Arthropoda.

The true position of the Polyzoa is as yet, as I have already said, a matter of doubt; but the arguments of Morse, and still more the recent investigation of Kowalewsky into the development of the Brachiopoda, place the close affinity of the latter with the Annelida in a clear light. The free larva of *Argiope*, for example, is wonderfully similar to those of *Spio* and of *Spirorbis*; and the mantle of the Brachiopoda appears to correspond with the cephalic hood of these Annelids. When it first becomes fixed, on the other hand, the young Brachiopod has many resemblances to *Loxomma* and *Pedicellina* among the Polyzoa.

As regards the Mollusca proper†, the larvæ of the Lamelli-branchiata, and of the majority of the Odontophora, have their parallel in the larva of the Annelidan *Phyllodoce*, while the young of *Dentalium* and of the Pteropods correspond with the larvæ of other Annelids. A Mollusk appears to me to be essentially an Annelid which is only dimerous, or trimerous, instead of polymericous.

The development of the perivisceral cavity in the Molluscan series stands much in need of elucidation. There seems to be little reason to doubt that the higher Mollusks are Schizocœlous;

* The like absence of cilia is a notable peculiarity of *Hirudo*, among the Leeches.

† See Mr. Lankester's valuable paper "On the Development of *Lymnæus*," Quarterly Journal of Microscopical Science.

but it is possible that the lower forms are Enterocœlous, like the members of the next division*.

The *Enterocœla*.—Kowalewsky has shown that in the Chætonognatha, represented by the strange and apparently anomalous *Sagitta*, the vitellus undergoes complete segmentation, and is converted into a vesicular *Morula*, on one side of which invagination takes place, and gives rise to the primitive alimentary canal, of which the opening of invagination becomes the permanent anus, the mouth being formed, by perforation, at the opposite end of the body. Before the mouth is formed, however, the primitive alimentary cavity throws out, on each side, a cœcal pouch, which extend as far forward as its central continuation; while posteriorly these pouches stretch behind the anus, meeting, but remaining separated by their applied walls, in the median plane of the body. These lateral sacs are next shut off from the median portion of the primitive alimentary cavity, which becomes the permanent alimentary canal; and they are converted into closed sacs, the cavity of each of which forms one half of the perivisceral cavity, while the inner wall, applied to the hypoblast, gives rise to the muscular wall of the intestine, and the outer wall, applied to the epiblast, becomes the muscular wall of the body, and gives rise to the generative organs. The great ganglia and nerves are developed from the cells of the epiblast. We have thus an animal which is temporarily cœlenterate, but in which the two gastrovascular sacs, enclosing what may be termed an "enterocœle," become shut off and metamorphosed into parts of exactly the same order as those which arise from the mesoblast of an Annelid. But it is not altogether clear whether the cells of the enterocœle in this case give rise only to the lining of the perivisceral cavity, and whether the muscles and connective tissue are in fact derived from the

* When I wrote this paragraph, I had been for some time in possession of the recent important memoir on the development of the Brachiopoda by M. Kowalewsky, as that distinguished embryologist had been good enough to send it to me. But it is written in Russian, and I could only judge from the figures that the perivisceral cavity of *Argiope* is developed in the same way as that of *Sagitta*. Some little time ago, however, my friend Mr. W. F. Ralston kindly took the trouble to translate so much of the text as referred to these figures for me, and I found that my interpretation of them was correct. The Brachiopoda, or some of them, therefore, are Enterocœla; and their relations with the schizocœle Annelida and Mollusca bring up anew the question suggested by the frequent origin of the mesoblast from the hypoblast (as in the Sharks for example), May not the schizocœle be derivable from a primitive enterocœle condition?

epiblast or not. Kowalewsky's evidence, however, is in favour of the origin of the muscles directly from the cells of the mesoblastic diverticula.

The brilliant investigations of Johannes Müller upon the development of the Echinodermata, confirmed in their general features by all subsequent observers, have proved, first, that the ciliated embryonic *Gastræa* (the primitive alimentary canal of which is formed by involution of a vesicular blastoderm), to which the egg of all ordinary Echinoderms gives rise, acquires a mouth by the formation of an aperture in the body-wall distinct from the primitive aperture of the *Gastræa*, so that, in this respect, it differs from all Coelenterata; secondly, that the embryo thus provided with mouth, stomach, intestine, and anus acquires a completely bilateral symmetry; thirdly, that the cilia with which it is primitively covered become restricted to one or more circlets, some of which encircle the axis of the body, or a line drawn from the oral to the anal apertures; and, fourthly, that within this bilaterally symmetrical larva or *Echinopædium*, as it may be called, the more or less completely radiate Echinoderm is developed by a process of internal modification.

Müller believed that the first step in this process was the ingrowth of a diverticulum of the integument, as a hollow process, out of which the ambulacral vascular system of the Echinoderm took its rise. He did not attempt to explain the origin of the so-called blood-vascular system (or pseudohæmal vessels), nor of the perivisceral cavity. Müller's conclusions remained unchallenged until 1864, when Prof. Alexander Agassiz took up the question afresh, and, in a remarkable paper on the development of the genus *Asteracanthion*, detailed the observations which led him to believe that the ambulacral vessels do not arise by involution of the external integument, but that they commence as two primitively symmetrical diverticula of the stomach (the "würstformige Körper" of Müller), one of which becomes connected with the exterior by an opening (the "dorsal pore" observed by Müller, and considered by him to be the origin of the ambulacral vessels), and gives rise to the ambulacral vessels, the ambulacral region of the body of the Echinoderm being modelled upon it; while, upon the other gastric sac, the antambulacral wall of the starfish-body is similarly modelled. Both gastric sacs early become completely separated from the stomach of the *Echinopædium*, and open into one another, so as to form a single horse-

shoe-shaped sac connected with the exterior by a tube which is converted into the madreporic canal. Agassiz does not explain the mode of formation of the perivisceral cavity of the starfish, and has nothing to say concerning the origin of the pseudhæmal vessels.

Recently Metschnikoff has confirmed the observations of Agassiz, so far as the development of the ambulacral system from one of the diverticula of the alimentary canal of the starfish larva is concerned; and he has added the important discovery that the perivisceral cavity of the Echinoderm is the product of the rest of these diverticula. Moreover his observations on other Echinodermata show that essentially the same process of development of the peritoneal cavity occurs in Ophiuridea, Echinidea, and Holothuridea.

The precise mode of origin of the pseudhæmal system, or so-called blood-vessels, of the Echinoderms is not yet made out. But it is known that the cavity of these vessels contains corpuscles similar to those which are found in the perivisceral cavity and in the ambulacral vessels, and that all of these communicate together.

Agassiz and Metschnikoff alike, justly insist upon the correspondence in development of the lateral gastric diverticula of the *Echinopædium* with that of the trunks of the gastrovascular system of the Ctenophora; and, on the ground of this resemblance, the former refers the Echinoderms to the Radiata, retaining under that Cuvierian denomination the Acalephæ (Cœlenterata) and the Echinodermata. But this arrangement surely ignores the great value of his own discovery, which shows that the Echinoderms have made a great and remarkable progress in passing from their primarily cœlenterate stage of organization to their adult condition. And it further ignores the unquestionable fact, admirably brought out by the same able naturalist's investigations into the development of *Balanoglossus*, that the *Echinopædium* is almost identical in structure with the young of animals, such as the Gephyrea and Enteropneusta, which are in no sense radiate, but are eminently bilaterally symmetrical. In fact, the larva of *Balanoglossus*, the sole representative of the Enteropneusta, was originally described by Müller under the name of *Tornaria*, as an Echinoderm larva, and was subsequently more fully examined by Prof. Alex. Agassiz, who also regarded it as an unquestionable Echinoderm larva; and it is only recently that it has been proved, partly by Metsch-

nikoff and partly by Agassiz himself, to be the larval form of *Balanoglossus*. In *Balanoglossus*, as in the Echinoderms, saccular diverticula of the intestine appear to give rise to the perivisceral cavity and its walls. In the Chætognatha, Echinodermata, and Enteropneusta, therefore, the perivisceral cavity is a portion of the alimentary cavity shut off from the rest; and in contradistinction to the Schizocoela, in which the perivisceral cavity is produced by a splitting of the mesoblast, they may be said to be Enterocoela.

The *Epicœla*.—In the Ascidiæ, the investigations of Kowalewsky, now confirmed in all essential points by Kupffer, have shown that the alimentary cavity is formed by the invagination of the vesicular *Morula*, that the blood-channels answer to the blastocœle, that the central nervous system is produced by invagination of the epiblast, as in the Vertebrata, and that, in most, the mesoblast of a caudal prolongation gives rise to an axial column flanked by paired myotomes, which are comparable to the notochord and myotomes of the vertebrate embryo*.

In the simplest Ascidiæ (the *Appendiculariæ*) the modified pharynx, which constitutes the branchial sac, is perforated by only two apertures, which open on the hæmal or ventral face of the body, and there is no atrial chamber. But in all other Ascidiæ an invagination of the epiblast takes place on each side of the anus, and, extending alongside the branchial sac nearly as far as the endostyle, give rise to a spacious chamber, lined by the so-called atrial or "third" tunic. In many Ascidiæ the chamber extends much further, so that even the alimentary canal and the generative organs are situated between the atrial tunic and the ectoderm. In this manner a kind of "perivisceral cavity" is formed, which is of a totally different nature from the "schizocoele" of the Annelid, and from the "enterocoele" of the Echinoderm, and which may be termed an epicœle.

The resemblance of the simplest of vertebrated animals, the Lancelet (*Amphioxus lanceolatus*), to the Tunicata was first indicated, though, it must be admitted, very vaguely, by Goodsir†.

* It is with great diffidence that I venture to express my dissent from the views of my venerated friend Von Baer, from whose works I first gathered sound principles of morphological science, and whose authority in such a matter as this has no equal; but I cannot think that the doubts he has expressed respecting the fundamental similarity between the Ascidiæ and the Vertebrata are warranted.

† "On the Anatomy of *Amphioxus lanceolatus*." Read before the Royal

In 1852 I gave full reasons for believing that the branchial sac of the Ascidian “represents, not the gill of the Mollusk, but the perforated pharynx of *Amphioxus*” *; and I described the development of the muscles of the tail in the larval Ascidian as “closely resembling that of the muscles of the Tadpole;” but in the absence of any sufficiently detailed knowledge of the development of the embryo of either the Ascidian or of *Amphioxus*, it was impossible to know what weight ought to be attached to these resemblances; and it was not until the publication of the memoir of Kowalewsky on the development of *Amphioxus* that their real significance became manifest.

In this animal, in fact, yelk-division gives rise to a vesicular *Morula*, which becomes provided with an alimentary cavity by invagination, and with a cerebrospinal axis by the development of laminae dorsales and the invagination of the corresponding portion of the epiblast, as in other Vertebrata.

The branchial clefts are secondary perforations of the body-wall and pharynx; and the protovertebrae and notochord are developed, as in Annelids and Arthropods, out of a mesoblastic layer situated between the epiblast and hypoblast, and therefore in the blastocœle. But one of the most important points made out by Kowalewsky is, that the branchial clefts at first open externally—and that they only acquire their anomalous position in the adult by the growth over them of two laminae of the body-wall, which

Society of Edinburgh, May 3rd, 1841, and published in vol. xv. of the ‘Transactions’ of that Society. “Viewed as an entire animal, the Lancelet is the most aberrant in the vertebrate subkingdom. It connects the Vertebrata, not only to the Annulose animals, but also, through the medium of certain symmetrical Ascidiæ (lately described by Mr. Forbes and myself), to the Molluses. We have only to suppose the Lancelet to have been developed from the dorsal aspect, the seat of its respiration to be transferred from the intestinal tube to a corresponding portion of its skin, and ganglia to be developed at the points of junction of one or more of its anterior spinal nerves and inferior branch of its second pair, to have a true annulose animal, with its peculiar circulation, respiration, generative organs, and nervous system, with supra-œsophageal ganglia, and dorsal ganglionic recurrent nerve.”

With every desire to give credit for sagacity where it is due, I think it is obvious from this passage, and from the fact that Goodsir denied the existence of the branchial clefts, or even of the abdominal pore, in *Amphioxus*, that he had no conception of its true morphological relations, and no valid grounds for the hint which he throws out.

* Report of the Belfast Meeting of the British Association, 1852. Transactions of the Sections, pp. 76, 77.

unite in the median ventral line for the greater part of their length, leaving only the abdominal pore open.

Although the structure of *Amphioxus* has been investigated by many able observers * during the last forty years, a reexamination of this singular animal, with which I first made acquaintance in 1846, has convinced me that some of its most remarkable morphological features have hitherto escaped notice; and I will take this occasion of laying a summary of the chief results at which I have arrived before the Linnean Society.

Amphioxus has hitherto been generally assumed to be a vertebrated animal, which differs from all others in possessing a mere rudiment of brain and of skull, and in being devoid of renal organs.

It is quite true that *Amphioxus* has neither brain nor skull, if we restrict the application of these terms to those particular forms under which the brain and skull are met with in the higher Vertebrata; but if we ask whether those regions of the cerebrospinal axis, and of the axial endoskeleton, which are metamorphosed into the brain and skull in the higher Vertebrata are, or are not, represented in *Amphioxus*, the answer must be, that these regions are not only present, but that, in relation to the size of the body, they are much longer than in any other Vertebrate, and that, in this respect, as in so many others, *Amphioxus* is the counterpart of the embryo of the higher Vertebrate.

The oral aperture of *Amphioxus* is surrounded by a series of tentacula; and the spacious buccal chamber is divided from the branchial one by a curiously arranged valvular "velum" (the "Franzen" of Müller). Close to the anterior end of the cerebrospinal axis is the ciliated olfactory sac discovered by Kölliker; and the pigment-spot, which represents the eye, coats the extremity of the same part of the cerebrospinal axis.

On comparing *Amphioxus* with the Lamprey, in its larval or *Ammocetes* condition, the cerebrospinal axis of the latter is seen to be a mere rod, somewhat enlarged at its anterior end, where it bears a mass of pigment representing the eye, and connected, by a very short cord, with a single ciliated olfactory sac. The oral aperture of the *Ammocetes* is also surrounded by tentacles; and, as in *Amphioxus*, leads into a wide buccal cavity, which is separated from the branchial sac by two remarkable folds, originally

* I need only mention the names of Retzius, Rathke, Müller, Goodsir, and Quatrefages. Within the last two years Stieda has published an elaborate paper on *Amphioxus* in the Transactions of the Academy of St. Petersburg.

described by Rathke, which answer to the velum of *Amphioxus*. But the dorsal ends of the attached edges of these folds are situated immediately under the middle of each auditory capsule; and, in the adult Lamprey, they can be proved to correspond with the position of the hyoidean arch. In the *Amphioxus* their dorsal attachment corresponds with the anterior angulation of the intermuscular septum between the sixth and seventh myotomes, counting from the anterior end of the body. Hence, it follows that this septum answers to the hyoidean arch of the higher Vertebrata, and that the six myotomes in front of it represent six primary segments of the body, or somatomes. But the first of these lies behind the eye, whence it also follows that the region occupied by these somatomes answers to the region included between the optic foramen and that for the seventh nerve in the skull of an ordinary vertebrated animal, and that so much of the head of *Amphioxus* as lies in front of the hyoid region answers to the præauditory moiety of the skull in other Vertebrata.

In *Amphioxus*, a nerve leaves the cerebrospinal axis in correspondence with the interval between each pair of myotomes, and then divides into a dorsal and a ventral branch, like an ordinary spinal nerve. And, in front of the first myotome, two nerves, or perhaps one nerve in two divisions, are given off. The more anterior of these two passes above the eye, and is distributed to the end of the body in front of the mouth, while the second and the other nerves pass to the side walls of the oral cavity.

These nerves, arising as they do between the homologue of the optic nerve and that of the *portio dura*, must represent the third, fourth, fifth, and sixth pairs of cranial nerves of the ordinary Vertebrata; while the myotomes between which five of them pass must represent the muscles of the nose, eye, and jaws. In fact, the course of the most anterior nerve is exactly that of the orbito-nasal nerve (the so-called ophthalmic, or first, division of the trigeminal), as is conspicuous when this nerve in *Amphioxus* is compared with the undoubted orbito-nasal of the Lamprey.

In the embryo Lamprey, at the most advanced stage described by Schulze, the portion of the centro-spinal axis which lies between the ear and the eye is relatively very long; but the cerebral hemispheres are beginning to grow out beyond the primitive anterior end of the cerebro-spinal axis, and project beyond the eye. In the young *Ammocetes* of 1.5 inch long the length is still great, though

it has not increased in proportion to the body; but the cerebral hemispheres are relatively larger, and the eyes are fully formed and have moved backwards, dividing the series of myotomes into a supraocular and a subocular bundle of muscles. And, in the adult Lamprey, changes in the same direction have gone still further.

It is clear, therefore, that the region occupied by the six most anterior myotomes of the body of *Amphioxus* answers to the præauditory region of the skull in the higher Vertebrata. The question next arises, How many of the succeeding myotomes are included in the region which corresponds with the postauditory or parachordal region of the skull in the higher Vertebrates?

The Lamprey has seven branchial sacs, with as many external clefts; and no Vertebrate ever possesses more. To each of these sacs nerves pass which undoubtedly correspond with the branchial branches of the glossopharyngeal and pneumogastric nerves; and strong grounds for thinking that the pneumogastric trunk contains the representatives of, at fewest, six primary distinct nerves, answering to the six posterior branchial sacs, have been given by Gegenbaur and myself. If this be so, then the seven pairs of nerves behind the representative of the portio dura in *Amphioxus* will answer to the glossopharyngeal and pneumogastric, and the eighth somatome will correspond with the occipital segment of the Ichthyopsida. Thus the skull of a Lamprey or of an Elasmobranch fish is represented by the anterior region of the body of the *Amphioxus* as far back as the fourteenth myotome. As there are from sixty to seventy myotomes, this estimate makes the head of *Amphioxus* to occupy, morphologically, one fifth of the whole body.

With respect to the renal organs, Müller thought he had observed some rounded bodies which might have a renal character in the posterior part of the abdominal cavity of living specimens of *Amphioxus*; but as he could not find them by dissection, and as no other anatomist has been more successful, they need not now be discussed.

Rathke described two canals situated in the ridges which are developed at the junction of the ventral with the lateral faces of the body. He states that these canals open, behind, at the abdominal pore, and in front at the mouth. Müller and, more recently, Stieda confirm Rathke's account, which appeared to be strengthened by Kowalewsky's statement that he had seen the ova pass

out by the mouth. Nevertheless there are no such canals. The ventro-lateral folds in question begin on each side of the front part of the mouth, and are continued along-side it, as Goodsir rightly states, becoming deeper as they pass back. At the sides of the abdominal pore, they terminate without uniting, one on each side of the præanal fin. In the living state, as well as in spirit specimens, these ventro-lateral laminae are strongly curved inwards; and they meet, or nearly meet, in the middle line, more or less covering the proper ventral aspect of the body, between the mouth and the respiratory pore. And it is simply the semicanals enclosed by these infolded ventro-lateral laminae which Rathke took for abdominal canals, open only in front and behind. The superficial layer of the integument, with its epiderm, is continued from the outer margin of each ventro-lateral lamina, over its edge, on to the inner surface of the lamina, and, in the normal state, is closely adherent to the greater part of that surface, becoming detached, to be reflected on to the proper ventral face of the body, only at the reentering angle between the ventro-lateral lamina and the ventral face. But, in spirit specimens, this superficial layer, which coats the inner face of the ventro-lateral lamina, sometimes becomes detached, along with more or less of its continuation on to the ventral surface of the body, and leaves a wide space, which is the abdominal canal described by Stieda, and erroneously supposed by him to be Rathke's canal. The floor of the respiratory chamber is formed by a layer of transversely disposed fibres, chiefly composed of muscular tissue and coated on the dorsal face by a layer of cells, forming part of the epithelium of the chamber. In the middle line these fibres are more or less interrupted by the raphe described by Stieda; the dorsal aspect of the floor is longitudinally grooved in correspondence with the raphe; and, not unfrequently, the epithelial cells dip down into this groove for a greater or less distance.

On the ventral face of the thick floor of the respiratory chamber the superficial layer of the integument is naturally separated by a narrow interspace from the transverse fibres of the floor, except in the middle line, where it is attached along a depression or groove corresponding with the raphe, like that of the dorsal aspect of the floor. This layer of integument is thrown into regular and close-set longitudinal plaits, which have been described as muscular fibres by Rathke, Müller, Goodsir, and Quatrefages. Stieda discovered the true nature of these longitudinal fibres; but his

figures give no idea of the regularity of the plaits, or of the manner in which the cells of the epidermis line the sides of the folds, which in transverse sections, have the appearance of glandular cæca. It is this organ which I conceive to be the renal organ, functionally, and to represent the Wolffian ducts, morphologically. These ducts are now known to be formed in the higher Vertebrates by involutions of the lining of that part of the peritoneal cavity which lies external to the generative area. Taking the raphe in *Amphioxus* to represent the line of union of the lateral laminæ, the development of which into the walls of the "perivisceral" cavity has been observed by Kowalewsky, the space between each lateral half of the plaited integument and the ventro-lateral fold of its side, will answer to an involution of the epithelium of the somatopleure, such as that by which the Wolffian duct of osseous fishes * commences; and the position of the reproductive gland low down on the wall of the somatopleure is in accordance with this interpretation.

On this view, the wall of the respiratory chamber of *Amphioxus* is strictly comparable to the somatopleure of a higher Vertebrate embryo. On the other hand, the cells which line it and represent the peritoneal epithelium must, from the mode of formation of the cavity, occupy the place of the epiblast, and represent a continuation of the epidermis. Thus the respiratory chamber of the *Amphioxus* is an *epicæle*, a cavity of the same fundamental nature as the atrium of the Tunicata; and this circumstance constitutes another curious point of resemblance between the Tunicata and *Amphioxus*.

On the other hand, it is such a cavity as would be formed by the growth and extensive union in the middle line of the lateral prolongations of the wall of the body in *Balanoglossus*.

To what does the respiratory chamber of *Amphioxus* answer in the higher Vertebrata? In the manner of its formation it corresponds, as I have elsewhere † suggested, very closely with the respiratory chamber into which the gill-clefts open in the Tadpole, and which, in most Anura, communicate with the exterior by only a single external opening on the left side of the body, though there are two symmetrical apertures in the Tadpole of *Dactylethra*. But, in its relations to the alimentary canal, and to

* Rosenberg, "Untersuchungen über die Entwicklung der Teleostier-Niere," 1867.

† Manual of the Anatomy of Vertebrated Animals, p. 121.

the generative and urinary organs, it is obvious that it no less closely answers to the "pleuroperitoneal"* chamber of the higher Vertebrates. The opercular fold which constitutes the outer wall of the branchial chamber in the Tadpole is formed by an outgrowth of the body-wall, as Kowalewsky states the wall of the respiratory chamber in *Amphioxus* to be. On the other hand, in all the higher Vertebrata, the somatopleure which bounds the "pleuroperitoneal cavity" seems to be formed by a sort of splitting by the mesoblast, apparently very similar to the process which gives rise to the perivisceral cavity of Annelida and Arthropoda. And the discovery of the free communication of the great serous cavities with the lymphatic system, has removed the objection that might have been urged that the serous cavities of the Vertebrata are not parts of the vascular system.

But it has been seen that it is only by the most careful study of development that the "enterocœlous" "perivisceral cavity" of the Echinoderm has been shown to be morphologically distinct from the "schizocœlous" "perivisceral cavity" of an Annelid; and I think it probable that renewed investigation will prove that the "splitting of the mesoblast" in the Vertebrata represents the invagination of the epiblast in the Ascidian, and the formation of an epicœle by outgrowth of a ridge in *Amphioxus*. Provisionally, at any rate, this hypothesis may be adopted, and the Vertebrata in general, as well as *Amphioxus*, ranked among the Epicœla.

The discovery of the true head, brain, and renal organs of *Amphioxus* removes the chief supposed anomalies of the structure of this animal, and to so great an extent bridges over the supposed hiatus between it and the Marsipobranchii, with which the development of the latter shows it to be very closely related, that I see no reason for separating it from the class Pisces, in which, however, it may properly rank as the type of a distinct order, which may be termed *Entomocrania*, in contradistinction to the rest, in which, as in all the higher Vertebrates, the skull, even in the embryonic state, exhibits no indication of its primitive segmentation †, and which may be termed *Holocrania*.

* More accurately "pericardio-pleuroperitoneal" chamber, as the pericardium is only part of it, and, indeed, is only incompletely shut off in the Rays and Myxinoid fishes.

† See the proof of this position in my Croonian Lecture, 'Proceedings of the Royal Society,' 1858.

The eye-spots of *Amphioxus* were single in all the specimens I have examined; in the very young *Ammocoetes*, described by Schulze, there are two such pigment-spots, separated by the very short representatives of the cerebral hemispheres and olfactory lobes. This suggests that the eye, like the nose, was primitively simple in the Vertebrata, and that it has become divided in the same way as the nose. In this case the involution of the epiblast, out of which the cornea and the crystalline lens are developed, should have been primitively a median sac; and it is a curious circumstance that, in the very young tadpole, Mr. W. K. Parker, F.R.S., has described and figured a transverse groove connecting the eye-sacs.

I am unable to find any thing in the structure or mode of development of the Marsipobranchii which gives this group more than an ordinal value in the class Pisces. Their great peculiarities are the structure of the skull, the presence of a nasopalatine passage which opens posteriorly in the Myxinoids, and the existence of a large superior median brain-lobe.

As respects the first point, the skull is strictly comparable with that of the embryo of any higher Vertebrate, being composed of a parachordal occipital portion, of largely developed trabeculæ, and of auditory capsules. In the Lampreys the cartilaginous hyoidean and mandibular arches are represented, and the curious facial cartilages appear to me to be reducible to the type of the labial cartilages of the Elasmobranchs. The development of the olfactory organ of the Lamprey proves that the single nasal sac of *Amphioxus* is the homologue of the nasal sac of the Marsipobranchii (at least of that part which is lined by the Schneiderian membrane), to which, however, two olfactory nerves, produced apparently by the division of a primitively simple and median nerve, proceed. The term "Monorhina," applied by Haeckel to the Marsipobranchii, therefore, is not strictly applicable, and I cannot attach any great taxonomic value to the structure of the olfactory organs in this group. The external duplication of the nasal apertures in the higher Vertebrata appears to me to be chiefly due to the fact that, in them, the cerebral hemispheres are thrown out in front of the anterior cerebral vesicle, the front wall of which (the *lamina terminalis* of the third ventricle of the fully developed brain) corresponds with the anterior end of the cerebro-spinal axis of *Amphioxus*, and attains a large size and considerable downward

growth before the olfactory sacs are distinguishable. The regions whence the olfactory nerves will be developed are thus widely separated, and thrown to the ventral and lateral aspect of the head, before the Schneiderian membrane is differentiated. It must also be recollected that, when the naso-frontal process of the embryo appears, the olfactory sacs become connected with one another by a transverse groove, which is persistent in the Rays, and has the same relations as the middle of the olfactory sac of the Marsipobranchii would have if it were supposed to be transversely elongated.

Recent investigations lead me to think that the lower jaw is by no means wanting in the Marsipobranchii, though it presents a very curious modification. In the Ammocœte the hyoidean cleft, which has been overlooked, is present; and the manner in which the branchial filaments are developed leads me to believe that those which are first formed represent the external gills of the Elasmobranchii, Ganoidei, Dipnoi, and Amphibia.

I have formerly expressed the opinion that the naso-palatine canal of the Marsipobranchii represents the "primitive mouth" of the Vertebrata. The resemblance of the mouth of *Amphioxus* to that of an Ascidian renders this comparison questionable; but, on the other hand, it is a remarkable circumstance that the median nasal involution of *Amphioxus* corresponds very nearly, in its relation to the segmented mesoblast, with the oral aperture of an Arthropod or an Annelid; and it may be that the canal represents the ordinary invertebrate oral passage.

The dorso-median brain-lobe of the Marsipobranch appears to me to be represented in the higher Vertebrata by the peduncle of the pineal gland, which in the embryo is a hollow process of the roof of the anterior cerebral vesicle. It is particularly conspicuous in young Elasmobranchs.

In a few Metazoa, as in some small Rotifera and in the Gordiaceæ, the alimentary canal never becomes developed, although these animals clearly belong to groups in which the alimentary apparatus is normally formed, and may be safely regarded as modified Gastreæ. Whether the like is true of the Cestoidea, which are so closely allied with the Trematoda, and of the Acanthocephala, is not certain. Probable as it may be that these are Gastreæ with aborted digestive cavities, it may be well to bear in mind the possibility of their never having passed through the

Gastrula stage. It is conceivable that an opaliniiform *Morula* should, under completely parasitic conditions of life, have developed the organization of a Cestoid worm. At any rate, the contrary must not be assumed without good evidence; and to indicate the doubt, it may be well to establish a provisional group of *Agastreæ* for these forms.

I subjoin a tabular arrangement of the animal kingdom according to the views expressed in this paper, remarking, in conclusion, that, in my belief, the progress of knowledge will eventually break down all sharp demarcations, and substitute series for divisions.

ANIMALIA.

I. PROTOZOA.

i. MONERA.

Protamœbidæ. Protomonadidæ. Myxastridæ. Foraminifera.

ii. ENDOPLASTICA.

Amœbidæ. Infusoria flagellata. Gregarinidæ. Acinetidæ.
Infusoria ciliata. Radiolaria.

II. METAZOA.

A. GASTREÆ.

i. POLYSTOMATA.

Porifera (or Spongida).

ii. MONOSTOMATA.

1. Archæostomata.

a. Scolecimorpha.

b. Cœlenterata.

Rotifera. Turbellaria.

Hydrozoa.

Trematoda.

Actinozoa.

Nematoidea.

Hirudinea.

(Ctenophora).

Oligochæta.

2. Deuterostomata.

a. Schizocœla.

b. Enterocœla.

Annelida Gephyrea(?)
polychæta.
Arthropoda.

Brachiopoda. Enteropneusta,
Polyzoa (?). Chætognatha,
Mollusca. Echinodermata.

c. Epicœla.

Tunicata or Ascidioida.

Vertebrata.

B. AGASTREÆ (provisionally).

Cestoidea. Acanthocephala.